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TAXONOMY AND DISTRIBUTION OF THE HOLARCTIC DIVING BEETLE *LACCOPHILUS BIGUTTATUS* KIRBY (COLEOPTERA: DYTISCIDAE)

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Abstract.—Several authors suggest that the Palearctic *Laccophilus minutus* (Linneaus 1758) and the Nearctic *L. biguttatus* Kirby 1837 are synonymous. Our investigation confirmed the opinion of other authors that they refer to separate species. However, *L. biguttatus* is Holarctic and *L. strohmi* Thomson 1874 (Halsingland, Sweden) and *L. apicicornis* Reitter 1899 (northern Mongolia) are junior subjective synonyms (NEW SYNONYMIES). Available specimen data suggest that *L. biguttatus* has two centers of abundance: western North America and Mongolia + adjacent Russia.

This paper is part of a series of papers investigating taxonomic relationships of Holarctic species of Dytiscidae. These papers have grown out of the simple question: How many species of Dytiscidae are shared between the Palearctic and Nearctic regions? An unpublished list compiled from other publications showed in excess of 100 names of dytiscids are mentioned by one or more authors as having a Holarctic distribution. This investigation began with an exchange of specimens and convinced us that examination of type material was critical to the project and that some concepts of Nearctic and Palearctic species needed modification or adjustment. Interestingly many of the synonymies discovered were not on our original lists of potentially Holarctic species. Earlier papers in this series are Nilsson (1981a, b, 1983a), Roughley and Pengelly (1982), Larson and Roughley (1983), Nilsson and Larson (1984) and Larson and Nilsson (1985). The latter three references enumerate the major reasons for the taxonomic problems and we presently add to this list problems which can be solved by thorough and careful examination of type specimens as well as accurate and detailed characterization of the species involved.

Various authors (e.g., Zimmerman, 1970) have noted the similarity between the Palearctic species *Laccophilus minutus* (Linnaeus 1758) and the Nearctic species *L. biguttatus* Kirby 1837. Examination of reliably determined specimens of each taxon convinced us that these were indeed distinct species. However, for the sake of completeness, we decided to examine specimens of other Palearctic taxa to determine if other names might apply to this species. We discovered the synonymy proposed below. Furthermore, the scope of many of the problems of the taxonomy of Holarctic species are well illustrated by the example of *L. biguttatus* Kirby.

HISTORICAL REVIEW

The taxonomic history of this species is relatively long and complex. *Laccophilus biguttatus* Kirby was described in 1837 and is the oldest available name. Kirby did

not specify a type locality for his specimen but it is inferred to be "Boreal America" because Kirby's original description appeared in Richardson's Fauna Boreali-Americana. This work was quite inaccessible in North America and prompted Bethune's (1871:30) quotation of the original work. Presumably because of this and because of a lack of specimens for comparison, the leading North American coleopterists of their time, J. L. LeConte and G. H. Horn considered *L. biguttatus* as conspecific with one or two of the more common and better known species of the eastern Nearctic region. Even after access to the original description, Horn (1883:282) was not convinced that this taxon was in the correct genus when he stated ". . . This has been placed as a synonym of two other species at various times, but it is probably not a Laccophilus at all and seems to be a species of Hydroporus, perhaps allied to pulcher *Lec.*" Horn (1883:281) stated that he had seen the types of *almost* all of Kirby's species, however it is doubtful that he had seen the type of *L. biguttatus* because of his statement.

C. G. Thomson described *L. ströhmi* from Helsingland, Sweden in 1874 and *L. apicicornis* Reitter 1899, was described from northern Mongolia. Thomson's and Reitter's concepts were similarly inadequately understood by the leading European coleopterists. For example, Sharp (1882:821) treated *L. strohmi* as *incertae sedis* commenting that it might be a variety of *L. interruptus* Panzer [now known as *L. hyalinus* (DeGeer)]. Sharp (1882:289), on the other hand, treated *L. biguttatus* as a junior synonym of the Nearctic species, *L. proximus* Say, signified by use of the annotation "M.C." for the Munich Catalogue of Gemminger and Harold (1868) as a reference to this synonymy. It is curious that Sharp did not study Kirby's types lodged in the British Museum. It is clear from comments in some of Horn's and LeConte's papers that they fully expected Sharp would provide authoritative judgement on the status of Kirby's species, however, this was not done.

Fall (1917) described *L. inconspicuus* from Winnipeg, Manitoba, Canada and this may well have been due to Sharp's failure to mention *L. biguttatus* explicitly. Fall's name was the one used in North America until Balfour-Browne (1944) made it a junior synonym of Kirby's name after examination of Kirby's type specimen. In the Palearctic region distribution was slowly becoming the most widely used taxonomic character to distinguish between *L. strohmi* and *L. apicicornis.* However as the known ranges of these "species-names" extended more confusion resulted. For instance, from the Jakutsk region, Russia, Poppius (1905) listed the occurrence of *L. obscurus* var. *stroehmi* and five years later Zaitzev (1910) listed the name *L. apicicornis* for specimens from the same area.

Zimmermann (1930) treated *L. strohmi* as a variety of *L. minutus* and members were characterized as differing from the typical form in color and microreticulation. The same character states were used by Zimmermann for the separation of *L. apicicornis* and *L. minutus.* Gschwendtner (1939:23) discussed a variety of *L. minutus* from Swedish Lapland. Our subsequent examination of this specimen convinced us that it belongs to *L. biguttatus.*

Brinck (1942) first surmised that *L. strohmi* and *L. apicicornis* were closely related but he did not provide characters by which they could be separated. He conclusively demonstrated that *L. strohmi* was distinct from *L. minutus* in body shape, color, elytral sculpture and shape of the median lobe.

Zimmerman (1970) revised the Nearctic members of the genus *Laccophilus.* He

noted the similarity between *L. minutus* and *L. biguttatus* and suggested that the two may be conspecific. In his monograph, Zimmerman used some of the same character states as had Palearctic workers earlier; however, he assigned them differing levels of taxonomic value. For instance his statement (1970:194) that members of these two taxa are similar in sculpture is ambiguous. Adults of *L. minutus* have a finely impressed secondary reticulation as well as primary reticulation whereas specimens of *L. biguttatus* have only primary reticulation. Therefore Zimmerman must have negated such differences in sculpture as of low taxonomic value. In contrast, character states of elytral reticulation are interpreted as being of high taxonomic value by Brancucci (1983) in his revision of *Laccophilus* from the eastern Palearctic, Oriental and Australian regions and by other European taxonomists. Brancucci also discussed the similarity between *L. minutus* and *L. biguttatus* (as *L. apicicornis*) but maintained them as specifically distinct and assigned them to separate species groups of *Laccophilus,* based in part on differences of elytral sculpture.

The synonymy of *L. biguttatus* may not yet be complete. Feng (1937) described *L. uniformis* Feng based on two female specimens from Shan Hai Koan, Hopei, China. This name is preoccupied and Guignot (1942) has supplied the replacement name, *L. fengi.* This species is certainly very close to *L. biguttatus,* however, efforts by Brancucci (1983) and ourselves have failed to locate the type series.

TAXONOMY

Laccophilus biguttatus Kirby, 1837

Laccophilus biguttatus Kirby, 1837:69; Bethune, 1871:30; Horn, 1883:282; Balfour-Browne, 1944:345; Gordon and Post, 1965:12; Zimmermann, 1970:193; Larson, 1975:260.

Laccophilus americanus, ex parte, LeConte, 1850:214; Branden, 1885:20; *nec* Aubé, 1838.

Laccophilus proximus, ex parte, Melsheimer, 1853:31; Gemminger and Harold, 1868: 445; LeConte, 1870:398; Horn, 1872:127; Horn, 1876:150; Sharp, 1882:289; Zimmermann, 1920:25; *nec* Say, 1823.

Laccophilus ströhmi Thomson, 1874:535. **NEW SYNONYMY.** Thomson, 1885:18; Sahlberg, 1886:206; Sahlberg, 1900:14; Brinck, 1942:123; Lindroth, 1960:148; Charpentier, 1972:291.

Laccophilus interruptus var. *stroehmi,* Sharp, 1882:281; Branden, 1885:22.

Laccophilus apicicornis Reitter, 1899:198. **NEW SYNONYMY.** (see citations in Brancucci, 1983:283).

Laccophilus n. sp., Wallis, 1915:170.

Laccophilus inconspicuus Fall, 1917:164; Wallis and Larson, 1973:101.

Laccophilus minutus var. *ströhmi,* Guignot, 1931:508.

Laccophilus stroehmi, Strand, 1970:119; Silfverberg, 1979:6; Nilsson, 1983b:9; Hagenlund, 1984:104.

Diagnosis. Color varied, dorsal surface testaceous to pale brown and venter pale yellowish-brown to nearly all black. Elytra without distinct color pattern and with microsculpture single, luster rather dull. Antennae slightly thickened and with last seven segments darkened apically. Male without stridulatory file. Total body length 3.9 to 5.0 mm. Median lobe of aedeagus as in Figures 1–6.

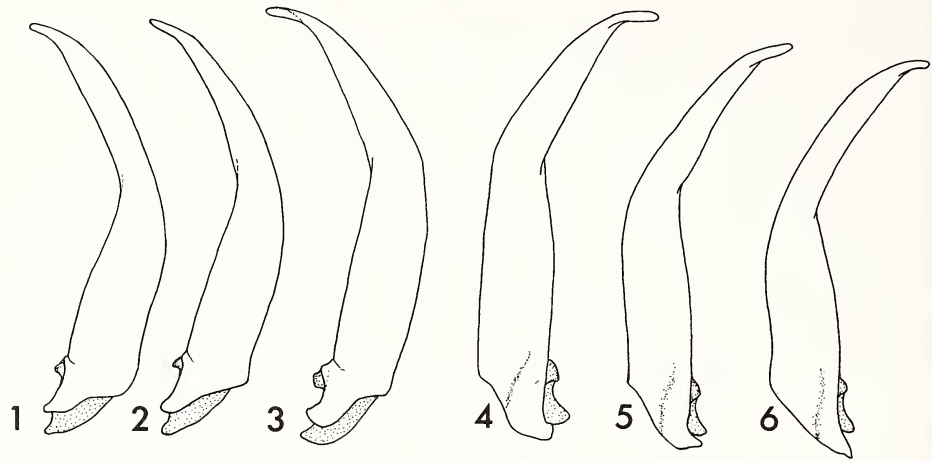

Fig. 1–6. Left and right lateral views of median lobe of aedeagus of male specimens of *Laccophilus biguttatus* Kirby (1 & 6, Canada, 2 & 5, Mongolia, 3 & 4, Norway).

Zimmerman (1970) gives a very good description of *L. biguttatus* and compares it to other Nearctic species. Brinck (1942) gives characters for its recognition in Europe (as *L. strohmi*), and, as *L. apicicornis,* it is well described and compared to members of the eastern Palearctic fauna by Brancucci (1983).

Notes about type material. The single specimen of *L. biguttatus* which Kirby examined is from North America and is deposited in BM [museum abbreviations follow Brancucci (1983:243–244), others are given in acknowledgments]. The holotype is a male and is labelled as follows: "Type/H.T./577la, N. Amer. (on underside of label)/ N. American/Laccophilus biguttatus Type Kirby."

The lectotype female of *L. ströhmi* Thomson (here designated by A.N.) is from Sweden and is labelled "Hsl. Str." and lectotype label. Paralectotype (here designated by AN.) labelled "Norl" and paralectotype label. Eight additional specimens were studied from C. G. Thomson's collection in UML.

The holotype of *L. inconspicuus* Fall, deposited in MCZ, is labelled "Winnipeg, vi-3-11/Type, inconspicuus/M.C.Z., Type, 23885/H.C. Fall, Collection." Details concerning the types of *L. apicicornis* Reitter, which is from northern Mongolia and deposited in BU are provided by Brancucci (1983:284). The latter were also examined by the junior author.

Material examined. All known locality records are mapped on Figure 7. Too many specimens from the Nearctic region were examined to list here. The following specimens were seen from Palearctic localities (arranged by country from west to east).
NORWAY: Aay, Gjerstad, Heilandsvann, 13 & 29.v.1983, G. Hagenlund (10, AN).
SWEDEN: Bohuslän, Spekeröd, 14.v.1984, B. Andrén (7, AN). Hälsingland, Ströhm (6, MNHG, 10, UML, 1, UZM). Jämtland, Ströhm (1, MNHG). Lule lappmark, Jokkmokk, Gschwendtner (1, OLM) Norrland, C. G. Thomson (1, UZM). Torne lappmark, Sappisaasi, 16.vii.1966, T. Karlsson (1, UML).
FINLAND: Kl, Jaakkaima, J. Sahlberg (1, UZM). Ok, Säräisneimi, 16.viii. 1947, Håkan Lindberg (11, UZM). Ob, Turtola, J. Sahlberg (1, UZM).

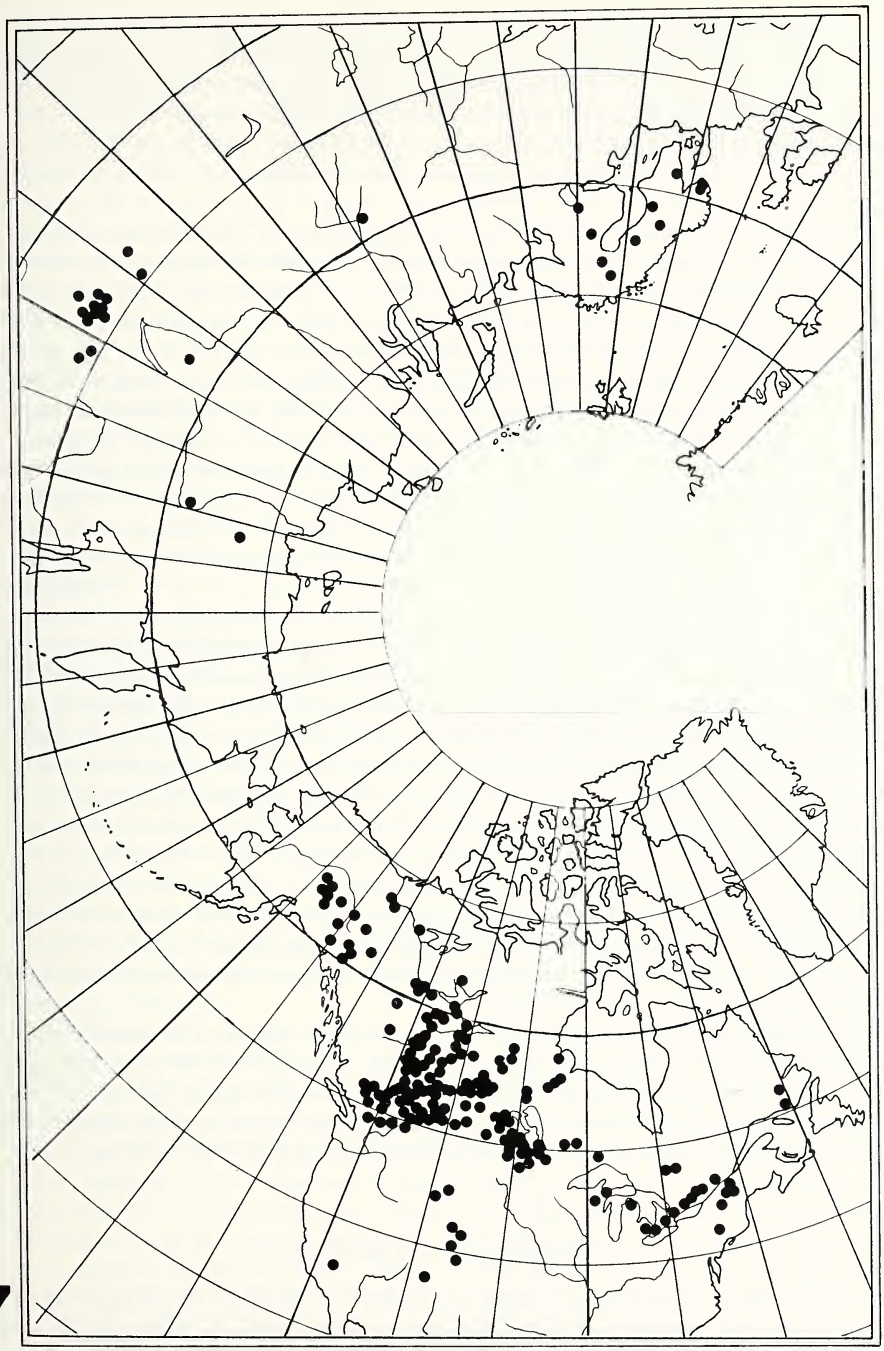

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Fig. 7. Distribution of *Laccophilus biguttatus* Kirby, locality records from specimens examined and literature.

RUSSIA: Russian SFSR, Leusch [=Leuši], Sundman (1, UZM). Samarovo [=Hanty-Mansijsk], (2, UZM). Tobolsk, Granö (2, UZM). Verchojansk, v & vi 1885, Bunge and Tol (3, ZIL). MONGOLIA: Changai, Leder (holotype and 3 paratypes, BU). Mongol. b., Uaga (1, ZIL), [locality not found]. Archangaj aimak, NO Ecke des Sees Ogij nur, 1,350 m, 2.vii.1964, Exp. Dr. Z. Kaszab, Nr. 249 (3, BU). Gobi Altaj aimak, ca. 30 km SO von Somon Zargalan, Fluss Zavchan gol, 1,700 m, 16.vii.1966, Exp. Dr. Z. Kaszab, Nr. 699 (2, BU).

Structural variation. Zimmerman (1970) and Larson (1975) discussed variation in color and size of this species based on North American specimens. We examined too few specimens from the Palearctic region to be able to generalize about color variation for this area. Adult specimens vary markedly in size. Zimmerman (1970) provided a range of total length for Nearctic specimens from 3.9 to 4.8 mm with smaller specimens being more common at the northern and southeastern limits of the range. All Palearctic specimens examined were within this size range. Mongolian specimens were between 4.2 and 4.6 mm whereas Scandinavian specimens are 4.2–4.8 mm. Interpopulation differences may be extensive however. Samples from Heilandsvann, Norway have a mean total length (MTL) of 4.68 mm (N = 10) while a sample from Spekeröd, Sweden which is only 250 km distant has an MTL of 4.35 (N = 7). Because of such interpopulation variation we have not been able to document any meaningful geographic pattern of variation. The ratio of MTL/MMW (mean maximum width), however, is about 1.8 for all samples measured.

The most notable variation of structure is in form of the median lobe of the aedeagus of male specimens (Figs. 1–6). Across North America, specimens (Figs. 1 and 4) are relatively consistent in form of the apex of the median lobe, the tip of which is a uniform extension of the pre-apical portion of the median lobe and is not differentiated. Most Siberian specimens of this species have a similar form of median lobe (see Brancucci 1983:417, figs. 153–154). In contrast, Mongolian specimens of *L. biguttatus* have the apex somewhat twisted (Figs. 2 and 4). In Scandinavian specimens the degree of torsion of the apex is greatest and therefore the undersurface of the tip of the median lobe can be seen in lateral view (Fig. 3) and the tip is therefore comparatively more differentiated (Fig. 6). While there are still large distributional gaps, we believe that the above variation is clinal and representative of separation of populations rather than species. Further study of specimens from intervening areas will support or deny our hypothesis.

Immature stages. Watts (1970) provided a short description of the third stage larva taken from acidic marshes at Delta, Manitoba. He described them as common in summer. Barman (1972) provided further details of life history and of third stage larvae from North America. Recently, Hagenlund and Nilsson (1985) have presented a detailed study of life history and immature stages in southern Norway.

DISTRIBUTION AND ABUNDANCE

The known distribution of *L. biguttatus* is shown in Figure 7. Records for localities are taken from Brancucci (1983), Guéorguiev (1965, 1968a, b, 1969, 1972), Larson (1975) and Zimmerman (1970) as well as the specimens listed above. Further Nearctic locality data are from CARR, CAS, CNC, CAS and JBWM. The following notes on

abundance and distribution are based primarily on field work in North America, on what can be inferred from specimen collection data, and from previous publications.

Several authors have discussed aspects of geographic distribution and abundance, in general and over entire species ranges (e.g., Preston, 1962; Hengeveld and Haech, 1982 and Brown, 1984, and references therein). In summary, species tend to be more abundant towards the geographic center of their ranges and less common at the periphery. Brown (1984) has suggested an explanation for non-normal distribution/abundance patterns and in particular bi- or multimodal patterns. We interpret *L. biguttatus* to have the latter type of pattern. There are three major centers of distribution based on locality information (Fig. 7): (1) Fennoscandia, (2) eastern Palearctic, in and around Mongolia, and (3) a transcontinental Nearctic component.

Most studies of distribution and abundance are based on precise sampling programs. Obviously we do not have such detail and accuracy in this case. Nevertheless it does seem profitable to analyze the known distribution of *L. biguttatus*. In the following discussion, we assume that there is a correlation between locality records (dots on Fig. 7), history and intensity of collecting (hereafter called collecting effort) and abundance. We believe that a relatively long history and intensity of collecting effort which results in few locality records is an indication of low abundance and low collecting effort which results in numerous locality records is indicative of increased abundance.

As noted above Fennoscandian records are geographically and temporally diffuse. The only record of large numbers of specimens is that of Hagenlund and Nilsson (1985). Therefore this "center" is probably due more to intensive collecting of populations on the edge of the range. We fully expect that additional records of *L. biguttatus* will better connect centers 1 and 2. The Mongolian group of localities (center 2) probably is much more indicative of abundance considering the comparatively reduced effort of collection. The majority of these records have resulted from Dr. Z. Kaszab's few expeditions to Mongolia and we interpret this as an indication of greater abundance of *L. biguttatus* in area 2. In North America, the distribution of dots on the map suggests that this species may be relatively abundant throughout much of the northern portion of the continent. However, in North America the total cumulative effort of collecting is very biased toward the northeastern United States and adjacent southeastern Canada. Therefore some further discussion of the Nearctic distribution is required.

In the Prairie Provinces of western Canada there are three major physiographic zones which may be broadly defined as (south to north) grasslands of the Great Plains, aspen parkland (mixture of grassland with *Populus* spp., etc.) and boreal forest. In this area specimens of *L. biguttatus* do occur sporadically on the grasslands, but are more commonly collected in parkland and forest habitats (Larson, 1975, 1985). For instance, Larson (1975) examined more than 600 specimens from the Province of Alberta where *L. biguttatus* was the second most frequently collected species (Larson, 1985) in his intensive study. In conjunction with its abundance this species occurred in a remarkable range of habitats and at a wide range of elevations. In increasing order of frequency of occurrence this species is known to inhabit: foothill marshes, saline ponds, warm streams and lakes, temporary grassland ponds, sphagnum bogs, boreal marshes and permanent grassland ponds (Larson, 1985). In addition, it can be found frequently in virtually any temporary site in the spring of the year (e.g.,

snowmelt puddles on sidewalks) which may indicate that this species exploits a range of temporary habitats during spring dispersal. Southward and eastward in North America this species is increasingly less commonly collected and apparently becomes restricted to habitats at higher elevations (Barman, 1972; Fall, 1917; Zimmerman, 1970). Similarly, this species is not known to as readily colonize temporary habitats towards the edges of its Nearctic range. For instance, the senior author has collected *L. biguttatus* at sporadic permanent habitats in southern Ontario, however this species was not found in the intensive studies of temporary ponds by Wiggins et al. (1980). James (1970) recorded this species from vernal woodland pools in Ontario but the abundance (James 1967) was notably reduced. In Ontario, at least, this species does not use temporary habitats to the same degree as in western Canada.

The range of habitats in which *L. biguttatus* has been collected in Mongolia is provided by Guéorguiev (1965, 1968a, b, 1969). The altitudinal range is from 700 to 1,700 m and members of this species occurred in temporary saline ponds as well as more permanent ponds in a forest. In Mongolia, *L. biguttatus* is apparently common in more saline habitats and along river margins; however, in general, the habitats are similar to the range of habitats known for Nearctic populations.

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